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SOME BOTANICAL AND ENVIRONMENTAL ASPECTS OF HAWAII

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Few regions anywhere are more interesting botanically than the Hawaiian Islands.

Owing to their extreme isolation, separated by 2,000 miles of ocean from the nearest land mass of any size, there is an extremely high percentage of endemic species, many of them remarkably specialized, testifying to the long period during which evolution has been going on with little disturbance from outside.

Except for the almost uniformly volcanic nature of the soils, which has no doubt been a factor in the evolution of the flora, the conditions are extremely varied. Owing to the great height of some of the mountains, which in the two great cones on the island of Hawaii, Mauna Kea and Mauna Loa, rise to nearly 14,000 feet, and overtop all the mountains of Polynesia and Australasia, there is a corresponding range of temperatures, from the tropical heat of the lowlands, to regions of almost perpetual snow. The variation in precipitation is also extraordinary, ranging between an annual rainfall of 400–500 inches in extreme cases,¹ to less than 20 inches in some of the dry leeward districts. These remarkable differences of elevation, temperature and moisture occurring within a quite small area afford the botanist unusual facilities for investigating a wealth of extraordinarily interesting problems in plant evolution.

The writer has made several visits to Hawaii, the last in the summer of 1919. Two years before, a trip was made for the purpose of collecting Hepaticae for comparison with certain East Indian species which indicate an interesting similarity in the hepatic floras of the two regions. This led to a somewhat critical study of the Hawaiian flora as a whole, which revealed an unexpected and most remarkable affinity with that of the Australasian and Indo-Malayan regions. So many were the correspondences that they led inevitably to the conclusion that these could only be explained satisfactorily by assuming the existence of some ancient land connections which have disappeared in a great general subsidence of the whole Polynesian area.

¹ A five years' record on Mt. Waialeale, Kauai, showed an average annual precipitation of a little over 500 inches. See *Science* for November 23, 1917, pp. 511–512.

The results of these studies have been published already² and will not be enlarged upon here.

The Hawaiian Archipelago consists of a chain of islands extending from northwest to southeast, between lat. $18^{\circ} 55'$ and $21^{\circ} 15'$. Its total area is 6,454 sq. mi., of which nearly two thirds is comprised in the southernmost island, Hawaii. To the N.W. a long series of small islets or reefs extends for about 18 degrees. All the islands, except for the coral reefs are volcanic; but at present the volcanic activity is restricted to the island of Hawaii, which has two enormous active craters, where the process of mountain building can be seen at any time. Volcanic outbursts of spectacular proportions have been a feature of the past two years, and last September a large lava flow burst out of the flank of Mauna Loa, and finally reached the sea, where it built out a promontory of considerable size.

In the older islands all activity ceased long ago, and the disintegration of the volcanic soils is complete; but in Hawaii, and to a lesser degree elsewhere, there are large expanses of bare lava, nearly or quite destitute of vegetation. The volcanic activity has evidently developed along a rift beginning at the northern end of the present chain of islands, and has proceeded southward, where it is now seen in the active craters of Hawaii.

There is strong evidence that all the large islands were once united into a single much larger land-mass, which through subsidence has gradually segregated the islands as they now exist. The northernmost island, Kauai, was the first to be detached, this being indicated, both by the deep and broad channel between it and its neighbor to the south, Oahu, and by the very highly specialized nature of its flora. The proportion of endemic species is higher in Kauai than in any other island, although it is one of the smallest.

The topography of the islands, especially the older ones, is excessively rugged. The windward districts are drenched with torrential rains, deposited by the moisture-laden North East trades. The resulting erosion has made innumerable deep and precipitous canyons, whose walls are often almost perpendicular. These vertical cliffs, "palis," whose brinks are often concealed by dense vegetation, make it very dangerous to wander about without a reliable guide.

In the older islands the mountains are much worn down and the highest summits are only 4,000–5,000 feet in elevation. The great cones of Maui and Hawaii, the most recent of the islands, however, are much higher, Haleakala on Maui being about 10,000 feet high, and Mauna Loa and Mauna Kea on Hawaii, nearly 4,000 feet higher.

On these lofty islands nearly all the moisture is precipitated on the windward (N.E.) side, while in the less elevated islands, much of the moisture is carried over the summits of the mountains and precipitated on the leeward

² "The Derivation of the Flora of Hawaii." Leland Stanford Junior University Publications, 1919.

side. This is seen very clearly back of Honolulu, where the heaviest precipitation is at the head of the valleys on the leeward side of the mountains. The leeward shores are relatively dry, and even arid in many places, so that the contrast between the scant vegetation of the sun-baked lee shores and the rank vegetation of the upland bogs and rain forest is sufficiently striking.

Little is left of the indigenous vegetation of the lowlands, except in some of the most barren districts—and even in these, exotic species have to a great extent driven out the native. Thus in some of the waste rocky districts near Honolulu, prickly pear cactus has taken almost complete possession. Practically all of the arable land of the lower levels is under cultivation, the huge plantations of cane and pineapples monopolizing most of the land not occupied by rice-fields, taro patches and home gardens. Most of the conspicuous trees, shrubs and weeds are introduced, and give to the casual observer an entirely erroneous impression of the native flora. In the neighborhood of Honolulu, for instance, the two most conspicuous trees are the Algarosa (*Prosopis* sp.) and Iron wood (*Casuarina equisetifolia*). Both of these are of comparatively recent introduction, but have become completely naturalized and have all the aspect of being indigenous. It is highly probable, also, that the cocoanut palms were introduced by the natives when they invaded the islands. Many foreign weeds have become thoroughly established, and in the hills back of Honolulu almost impenetrable thickets of Guavas and Lantana have taken possession, while in the driest places the prickly pear and thorny acacias thrive. In the moister parts of the islands some very attractive exotics have become naturalized. Wild ginger (*Hedychium coronarium*), *Canna indica*, *Clerodendron* sp., Ipomoeas, and passion flowers are common along the roadsides and in the woods about Hilo and in the rainy valleys back of Honolulu, and elsewhere.

The strand flora includes such widespread types as *Hibiscus tiliaceus*, *Ipomoea pes-caprae*, *Scacvola frutescens*, Pandanus, and Calophyllum,—all types familiar to anyone acquainted with the strand vegetation of the Eastern tropics and the South Seas; but the strand flora as a whole is very poor when compared with the latter regions. There is a considerable number of endemic strand plants, but these are, as a rule, not very common, and are often very much restricted in their range.

While little is left of the lowland native vegetation, except for the strand flora, the forests, where they have not been destroyed—intentionally or otherwise—harbor many very peculiar indigenous trees and shrubs, as well as a rich flora of ferns, liverworts, mosses, lichens and fungi. Herbaceous flowering plants are relatively scarce.

The predominant trees of the lower forest are two—the “Kukui” (*Aleurites Moluccana*), and the “Ohia” or mountain apple (*Eugenia Malaccensis*). The former is very conspicuous on account of its pale silvery green leaves, which contrast strongly with the dark green foliage of the

other forest trees. Its oily seeds were formerly much used by the natives. The showy red fruits of the Ohia are very refreshing and are relished by the white inhabitants as well as the natives. As both the Kukui and Ohia are of considerable economic value, and as they are common in the South Pacific regions, it may well be that their seeds were brought to Hawaii by some of the early native immigrants.

The upper forest zone—3,000–4,000 feet, especially on the windward side of the islands, is a pronounced rain forest, with dense undergrowth and many epiphytes. These include numerous ferns, among them several species of filmy ferns, the big bird's nest fern (*Asplenium nidus*)—*Ophioglossum pendulum*, several species of Lycopodium and various other forms. The lianas are not abundant, the most conspicuous being a Freycinetia, which, however, is more abundant at lower elevations.

The predominant tree of all the higher forest is *Metrosideros polymorpha*, which is extremely adaptable, as it occurs at all altitudes from near sea-level to more than 4,000 feet in elevation. The showy red flowers are produced in great profusion and are assiduously visited by some of the honey-sucking birds belonging to the peculiar Hawaiian family Drepanididae.

An examination of the trees and shrubs of the lower forest zone will show that many of the genera are characteristic of the South Pacific regions, Australasia, and Indo-Malaya. Pandanus and Freycinetia represent the Pandanaceae, quite absent from America, and many others are members of extra-American genera. Among these are Pittosporum, Gardenia, Coprosma, Metrosideros, Santalum, Cyrtandra, Dracaena and others. This affinity of the flora with the regions to the south is shown also by the Pteridophytes and Hepaticae.

The preponderance of Old World and Australasian genera, and the paucity of American types, is the most remarkable feature of the vegetation as a whole.

As in all tropical mountain forests ferns constitute a conspicuous part of the vegetation. Tree ferns of the genus Cibotium abound in all the rain-forests, and are especially fine in the mountain forests of Hawaii. The peculiar Hawaiian genus Sadleria develops a short trunk, but is much inferior in size to Cibotium. The Marattiaceae are represented by a single species, *Marattia Douglasii*. There are several species of Ophioglossum, including the striking epiphytic *O. pendulum* and several species of Gleichenia are abundant. There is a single species of Schizaea, and several Hymenophyllaceae, in addition to a large number of Polypodiaceae.

There are no Gymnosperms, and several widespread tropical genera that one would expect to find are absent. Most noticeable perhaps is the absence of any native species of Ficus, one of the most widespread genera of trees. The Orchidaceae are very poorly represented, only three species being recorded from the Islands, and there are no Araceae that can with certainty be considered as truly indigenous.

There are a good many endemic genera, mostly trees and shrubs, belonging to several families. Among these are *Platydesma* (Rutaceae), *Pterotropia* and *Cheirodendron* (Araliaceae), *Gouldia* and *Straussia* (Rubiaceae), *Raillardia*, *Hesperomannia* (Caupositae). Perhaps the most interesting family, from the standpoint of evolution, is the Lobeliaceae. This family has developed in a most remarkable way in Hawaii, and contains some of the most striking members of the flora. The genus *Lobelia* is represented by a number of species, but it is the two endemic genera, *Clermontia* and *Cyanea* which show the most remarkable developments. Some of these are tree-like, the largest 10 metres or more in height, the tall stems sometimes unbranched, and terminating in a palm-like crown of huge lanceolate leaves, below which are clusters of curious flowers.

The only indigenous palms belong to the genus *Pritchardia*. These are small or moderate-sized fan palms, occurring on all the islands, but not in great numbers.

OAHU

The Island of Oahu, upon which is situated Honolulu, naturally has been most exhaustively studied botanically. The immediate vicinity of the city is entirely under cultivation, and practically nothing is left of the original vegetation. Back of the city, however, are several valleys indenting the low mountain range extending the greater part of the length of the island. At the heads of these valleys and above them, there still remains a considerable extent of forest, which harbors many of the interesting indigenous plants and gives a fairly good idea of the character of the original flora.

The main range of Oahu is low, scarcely exceeding 3,000 feet at its highest point, and the moisture-laden trade winds pass over the summit and deposit a large share of their moisture at the head of the valleys on the leeward side. There is a remarkable difference in rainfall between the head of these valleys, where it may reach 200 inches annually and the dry coastal district at their openings, only a few miles distant, where it may be less than one fourth as much.

Of the valleys back of Honolulu, one of the largest is Manoa, whose physiography and vegetation have been discussed at some length in a recent paper by McCaughey.³ The lower part of the valley is now part of the city, and even before this was the case, the floor of the valley had been taken up by the gardens and plantations of the natives, so that the native vegetation has long since disappeared. The head of the valley, however, still harbors much of the original forest, although the lower levels have been so ravaged by cattle and the inroads of wood cutters, etc., that most of the forest has disappeared and a jungle of guavas, *Lantana*, and other introduced shrubs and weeds have pretty effectually driven out the original growths. One of the worst weeds is the Hilo grass (*Paspalum conjugatum*), which rapidly

³ McCaughey, V. American Journal of Botany, 4: 561-603, December, 1917.

invades the least clearing in the forest and soon chokes out the ferns and other delicate plants which form the natural ground cover. The rank growth of the grass makes it impossible for most tree seeds to germinate, and the doom of the forest is sealed.

Where the lower forest still exists, it is composed largely of the Kukui (Aleurites) and Ohia (*Eugenia Malaccensis*) already referred to.

Above the Kukui zone is a region characterized by another important native tree, *Acacia Koa*, allied to the phyllode-bearing Australian species. Above the Koa zone is the rain-forest in which are found many of the characteristic native trees and shrubs, very largely endemic species. Among these are species of *Antidesma*, *Cheirodendron*, *Eugenia*, *Ilex*, *Hesperomannia*, *Metrosideros*, *Osmanthus*, *Pelea*, *Pittosporum*, *Pritchardia*, *Santalum*, *Suttonia*, *Straussia*, *Clermontia*, *Coprosma*, *Cyanea*, *Hibiscus*, and others.⁴ In this rain forest there is a rich growth, also of ferns, liverworts, and mosses.

The gardens of Honolulu are famous for their display of tropical and subtropical vegetation. One may see there most of the gorgeous flowering trees, shrubs and climbers of the tropics as well as many varieties of tropical fruits. A specialty of the Honolulu gardens is the great variety of *Hibiscus*. The scarlet *H. rosa-sinensis* has been crossed with some of the handsome native species and the result is a wonderful variety of most beautiful forms. The garden planted by the late Dr. Hillebrand, author of the *Flora of Hawaii*, still exists and contains magnificent examples of many rare palms and other tropical trees, some of really gigantic size.⁵

KAUAI

The northernmost island, Kauai, is the richest of the islands in number of species, and in the percentage of endemics. It is also the most productive in proportion to its size, the fertile soil and abundant water giving it the popular name of the Garden Island. The greater part of the area is occupied by an elevated plateau about 4,000 feet high, rising in the center of the island to 5,000 feet in Mt. Waialeale. The latter is, so far as records show, the rainiest spot in Hawaii, and certainly one of the wettest anywhere (see footnote 1). The region about Waialeale is occupied by grassy bogs and swampy forests of scrubby trees, which are extremely difficult to traverse as the writer can testify. The open bogs are much like those of northern regions and harbor many temperate plants, such as *Drosera longifolia*, *Sphagnum*, species of *Rubus*, *Vaccinium*, *Viola*, *Geranium*, and various coarse grasses and sedges. This region is also characterized by a number of single representatives of genera which according to Hillebrand belong in

⁴ For details see McCaughy, loc. cit.

⁵ For a detailed account of the ornamental trees, the reader may refer to Prof. J. F. Rock's "Ornamental Trees of Hawaii (Honolulu, 1917).

the Antarctic regions, New Zealand, Falkland Islands, and the Southern Andes.⁶

One of the most conspicuous plants of the wettest rain forest, found in all the large islands at elevations of 3,000 to 4,000 feet, is *Gunnera petaloidea* Gaud., which suggests a particularly luxuriant rhubarb, the huge leaves being 3 to 4 feet across, or even more. The genus is best developed in New Zealand, but has representatives in Chile and one species in the Malay Archipelago, but is not known elsewhere in Polynesia.

MAUI

Maui, the second in size of the islands, consists of two parts, East and West Maui, connected by a low isthmus. These two parts are of different ages. West Maui is evidently much older, and it is thought may have been connected, formerly, with the Kohala Mountains in N. E. Hawaii. The summit is almost 6,000 feet in height, and is occupied by bogs, said to be much like those in Kauai; and there are deep gorges on the windward side cut out by streams of considerable size.

East Maui is made up entirely of the gigantic volcanic mass of Haleakala, 10,000 feet high, with a huge extinct crater over twenty miles in circumference, and 2,000 to 3,000 feet in depth. Although there is no record of eruptions, there is every evidence that activity has ceased only in relatively recent times, and the lava flows within the crater look as if they had just been formed.

Much of the forest on the dryer slopes of Haleakala has been entirely destroyed by cattle, but in the wetter districts there are still dense rain-forests of the most pronounced type. These are best developed at about 4,000 feet elevation. Above this the precipitation is much less and the whole summit of Haleakala is decidedly arid.

HAWAII

From an ecological standpoint, Hawaii, much the largest of the islands, is perhaps most interesting, although it is much poorer in number of species than the older islands. A small district in the northeast corner is occupied by the low range of the Kohala Mountains, very much older than the rest of the island, and probably once connected with West Maui. The greater part of Hawaii is composed of three large volcanoes, Mauna Loa, Mauna Kea, and Hualalai. The former is still in activity, and has two enormous craters, one of which, Kilauea, is familiar to all the tourists who visit Hawaii. The summit crater is difficult of access and is seldom visited. Owing to the presence of this great active volcano, such problems as the effects of volcanic eruptions upon vegetation, the invasion of recent lava flows by plants, and the establishment of new plant societies, and kindred problems, can be

⁶ F. Hillebrand: "Flora of the Hawaiian Islands," Introduction, p. xxiv.

carried on in Hawaii as they can scarcely anywhere else. Owing to the great elevation of the mountains nearly all the moisture is precipitated on the windward side of the island, and much of the leeward or "kona" side is a desert of dead lava. Hilo, the principal town, is situated on the windward side, and the whole district is extremely wet, the annual rainfall in Hilo being not far from 200 inches. Being the most southerly of the islands, this great rainfall results in an extremely luxuriant vegetation and Hilo is decidedly the most tropical-looking place in all the territory.

Formerly covered with forest to the water's edge, the lower slopes of the mountains are now completely cleared, and up to 2,000 feet they are principally devoted to cane fields. Above this, owing largely to the ravages of cattle, the forests are rapidly disappearing.

The rain-forest is evidently very quickly affected by any disturbance of the balance of species, and the invasion of cattle or other herbivorous animal not only destroys the native undergrowth, but allows the intrusion of weeds, especially the Hilo grass, which quickly destroys the ground cover of ferns and other delicate plants, and makes it impossible for the forest to perpetuate itself, both because the trees cannot long survive this exposure resulting from the destruction of the undergrowth, and because the conditions for germination of their seeds have been destroyed. Very soon the trees die, and what was a dense jungle becomes an open waste of grass and weeds, with the shabby remnants of a few tree ferns, and the stumps and skeletons of dead trees (an example of forest destruction along the road from Hilo to the volcano is described below).

The destruction wrought by grazing is seen on a large scale on the slopes of Haleakala in Maui, and on the Waimea plains of Hawaii. In some parts of the Islands, goats have run wild, and are the source of much damage to the vegetation.

The effects of erosion on the windward side of Hawaii are very remarkable. From the steamer approaching the shore there are visible the openings of deep valleys, cutting through the high cliffs which fall perpendicularly into the sea. Not infrequently the stream which has cut the gorge forms a cataract over a high cliff into the ocean.

Through the kindness of Dr. H. A. Lyon of Honolulu, the writer had an opportunity of collecting at the head of the largest of these gorges, Waipio Valley, which extends into the Kohala Mountains, the oldest formation of the Island.

The head of Waipio gorge divides into several branches, whose almost sheer walls fall straight to the floor of the canyon, 3,000 feet below. The cataracts falling over these vertical cliffs, except for their lesser volume, recall some of the falls of the Yosemite Valley. A narrow trail skirted the brink of this tremendous chasm, and above it rose a rocky wall, indented here and there with little caves, and covered thickly with a wonderful profu-

sion of ferns, liverworts, and mosses, the liverworts in particular being extraordinarily abundant and luxuriant. Everything pointed to a tremendous rainfall, and we had a practical illustration in a succession of heavy showers which drenched us to the skin. At one place great cushions of *Sphagnum* were seen, an unusual sight in Hawaii, and beyond the gorge was an extensive nearly level boggy region, full of interesting plants, including a few specimens of a fan palm (*Pritchardia lanigera*). In this remote region very few introduced plants had got a foothold, the vegetation being almost entirely composed of truly indigenous species, among which were a number of interesting Lobeliaceae.

Very different was the aspect of the great Waimea plain, only a few miles from the Waipio gorge, and extending to the lower slopes of Mauna Kea. This region was formerly heavily forested but is now a treeless plain, the grazing ground for thousands of cattle.

The region about Hilo is very interesting botanically, although one has to go a long way to find the forest still standing. Owing to the great humidity, rain-forest types may be found near sea level, in gorges where remnants of the forest still remain. Filmy ferns, many liverworts, and species of trees and shrubs which usually grow at much higher elevations may be found. A remarkable instance was seen near Hilo. In 1881 a great lava flow almost reached the city, which was threatened with destruction. The great expanse of lava is still easily recognizable, although it is covered with the beginnings of a new forest. The roof of a large lava tunnel has broken through, forming a cave, open above, but well sheltered from the sun and wind. In this cave there is a luxuriant growth of ferns and liverworts, as well as some thrifty trees and shrubs, which have grown much better than their companions on the exposed lava above them.

Dr. Lyon pointed out a most interesting fact, viz., that practically all the plant colonists on the lava were strictly indigenous species. The introduced plants, like the weeds abounding along the roadside and in the cultivated land in the immediate vicinity, failed to obtain a foothold on the lava, while the indigenes seemed to find exactly the conditions they needed.

The most important element of the embryo forest is *Metrosideros polymorpha*, which quickly appears in Hawaii upon the recent lava flows. In the rain-forest, this tree most commonly begins as an epiphyte, especially upon tree-ferns, and often develops stilt-roots like those of many species of *Ficus*. As seems to be always the case in the colonizing of fresh volcanic soils, Pteridophytes play an important rôle. The characteristic fern, *Sadleria cyatheoides*, and species of *Lycopodium* and *Psilotum*, are among the early growths to appear; and a *Vaccinium*, with showy red and yellow berries, the "Ohelo" of the natives, is a common and conspicuous denizen of the lava.

A visit to the volcano was not without its melancholy aspects. When

the writer made his first visit to this remarkable place in 1892 the greater part of the road from Hilo was through a dense unspoiled rain-forest. In some of the lower forest the undergrowth had been partly removed for the planting of coffee but otherwise the forest was left intact, and there was most interesting collecting within a short distance of Hilo. Now all the lower forest has disappeared to make way for cane, which covers all the available land. Most of the forest along the volcano road has either been cut down or has been so ravaged by cattle and the consequent encroachment of Hilo grass and other weeds, that very little of it is left. The last forlorn stragglers of the myriads of tree ferns that formerly lined the road, are slowly dying, exposed to the sun and wind, and the skeletons of dead trees rise from a waste of tangled weeds and grass.⁷

The country about the crater of Kilauea is decidedly interesting botanically. It is much dryer than Hilo and further on becomes very barren. Much of the region about the crater is covered with recent lava flows upon which a sparse vegetation has developed which gives a fair index as to the age of the different flows. Occasionally quite heavily wooded patches are seen, showing areas that were surrounded by the lava-flows but escaped destruction. These islands of older vegetation, "Kapukas" in the native tongue, are very interesting features of the region about the volcano.⁸

The remains of a magnificent forest of Koa (*Acacia Koa*) still exist not far from the volcano, but this has been used as pasture and invaded by Hilo grass, so that apparently seedlings cannot get a start, as nothing but mature trees can be found. Twenty-five years ago there was a fine undergrowth of tree-ferns and other native plants, but these have pretty much vanished and it will not be long before the forest has disappeared unless steps are taken to restore something like the original conditions.

Of the rain-forest below the crater, little is left in the vicinity of the volcano. A few small tracts have been enclosed—notably one belonging to Mr. W. M. Giffard of Honolulu, who kindly permitted the writer to collect there. These enclosed tracts show what the forest was in earlier days. Especially striking are the beautiful tree-ferns—*Cibotium Menziesii* and *C. Chamissoi*—which formerly abounded throughout the forest regions between Hilo and the volcano. A profusion of small ferns, as well as dense growths of liverworts and mosses cover the trunks and lower branches and even the leaves of the trees and shrubs.

An unusual and interesting little collection of plants was met with close to the active crater. Steam vents opening into a rift near the wall of the

⁷ [This is a particularly good example of the influence of the "biological factor" of the environment. We have enough—and too many—cases of forest destruction in this country, but few in which the identical spot has been described both before and after the destruction occurred.—Ed.]

⁸ For a fuller account of the flora of the volcano region see Rock, "The Indigenous trees of Hawaii." Pp. 27-33. Honolulu, 1913.

crater produced a small natural hot-house, where the heat and moisture had caused quite a luxuriant growth. The wall of the fissure, close to the steam vents, was covered with a thick, slimy coating of several species of Cyanophyceae, which displayed various bright tints. On the ground were several ferns and other plants, including an *Ophioglossum*, which has not been found elsewhere at this elevation, but occurs at sea level in the warm lowlands.

Comparatively few of the native plants produce showy flowers, although there are some of marked beauty, such as several species of *Hibiscus* with large white or yellow flowers. Some species of *Lobelia* and *Scaevola* are quite showy, and the scarlet flowers of *Metrosideros* and the leguminous climber, *Strongylodon lucidum*, beloved of the honey-sucking birds, are very conspicuous. Near the volcano these birds are quite common, and when perched near the scarlet flower clusters of the *Metrosideros* it is not easy to distinguish the red bird from the red flowers. Most of these birds have a long curved bill, which seems specially adapted to probing the curved tube of the *Lobelias* and the long curved keel of the *Strongylodon*.

The great preponderance of Southern Pacific and Asiatic types in the Hawaiian flora is very evident. The writer has treated this topic at some fifty extra-American genera are common to Hawaii and the regions of the South Pacific and Indo-Malaysia, while the number of strictly American genera occurring in Hawaii is only six. There are nearly forty extra-American species of Pteridophytes common to Hawaii and the Australasian-Indo-Malaysian area, while only two peculiarly American species are known from Hawaii. The Hepaticae show much the same relations.

The animal life of the Archipelago shows much the same correspondence with the faunas of the Southern hemisphere as is shown by the floras of the two regions.

Various explanations have been offered as to the origin of the Hawaiian plants, based on the assumption that the Archipelago has always been completely isolated, and is of purely volcanic origin, having been thrown up from great ocean depths. The nature of the flora of the Islands is scarcely to be reconciled with such a theory, since a large proportion of the plants, whose nearest relatives are in Australasia and the Malay Archipelago, possess no provision by which they could have survived the long journey over four or five thousand miles of ocean. A large number of these plants, including such delicate forms as the filmy ferns and many liverworts, inhabit the cool rain-forests, and one finds it difficult to conceive any means of transport length in two earlier papers,⁹ and will not dwell upon it at length here. Over

⁹ Campbell, D. H.: "The Origin of the Hawaiian Flora." *Memoirs of the Torrey Botanical Club*, 17, 90-96-1918.

Loc. cit., 1919.

from distant New Zealand or the mountains of Java and New Guinea to the mountain forests of Hawaii which would enable the spores of these delicate plants to survive the exposure of such a journey.

It is evident that most of the forms have been in the Islands for a very long time, as a great majority are endemic, although related to species or genera in other parts of the world. The extraordinary degree of endemism is scarcely equalled anywhere else, and points to a long period of isolation since the introduction of the ancestors of the present flora. This long isolation has resulted in a good many endemic genera, as well as species.

The small number of American types is remarkable, inasmuch as there are agencies which might be expected to bring to the Islands a good many plant immigrants. A considerable number of birds are regular migrants from the West Coast of America, and the prevailing trade winds are from the same direction. Moreover ocean currents frequently bring drift from the Northwest American shores. None of these agencies can be called in to account for the transfer of seeds from the remote regions to the South, whence it is certain most of the plant life of the Islands has been derived.

It seems necessary, therefore, to assume some ancient, more or less direct, land communication with the regions of the Southern Pacific. There is good evidence of extensive subsidence in the Hawaiian Archipelago which has resulted in the formation of the separate islands that now exist. This is most strikingly borne out by the flora of Kauai, which it is believed was first cut off. The flora of Kauai is not only the richest in number of species, but the species are most highly specialized and many are found exclusively in this island, indicating an early separation of the island from the other members of the Archipelago.

The island of Hawaii offers a great contrast to Kauai. Many times larger, it is for the most part made up of recent volcanic formations, a considerable part of which are still almost destitute of vegetation. The flora of this great Island, except in the small area occupied by the ancient Kohala range, is much less varied than that of the older islands, and comprises relatively few species, which are not found in the other islands.

A similar subsidence probably has occurred throughout Polynesia, and it is likely that at some remote period, perhaps in the early Tertiary, there existed one or more large land masses over what is now Polynesia, the existing islands being the summits of sunken mountain masses.¹⁰

It is known that the Malayan Archipelago was once united with the Asiatic mainland, and that the southern extremity of the American continent was connected in some fashion with New Zealand. The remarkable simi-

¹⁰ [An interesting piece of work on this subject is H. P. Crampton's "The Zoological Facts of Distribution in Relation to the Problem of Subsidence in Polynesia," not yet published, and his "Studies on Variation, Distribution and Evolution of the Genus *Partula*; the Species Inhabiting Tahiti," Carnegie Inst. of Washington, Publ. 228, 1917.—Ed.]

larity between the floras of Hawaii and these southern land masses indicates, in the opinion of the writer, that the existing flora of Hawaii is in large part descended from types which were widespread over the great land areas which in Tertiary time, perhaps, connected Hawaii with the ancient continents of the South Pacific. These ancestral forms, in the course of ages have become much altered in many cases, but others have persisted with but little change. Presumably a good many forms have become extinct, and a considerable number of new ones have been introduced from outside. This is probably true of all the species which are allied to types from the Pacific Coast of North America. The time when the isolation of the Archipelago became complete must be largely conjectural, but to judge from the character of the fauna, it may well have been in the Mid-Tertiary or possibly somewhat earlier.

We may then conclude that the bulk of the vegetation in Hawaii is made up of residual types, *i.e.*, remnants of a flora common to the ancient much larger Hawaii, and the continental masses to the South. These ancient types have become more or less changed since the isolation of the Archipelago, and their number has been augmented by a relatively small number of forms introduced from America subsequent to the isolation of the Islands.

SUMMARY

The Hawaiian islands present extremely varied environmental conditions: mountains nearly 14,000 feet high give temperatures ranging from tropical heat to almost perpetual snow; the yearly precipitation ranges from less than 20 to over 500 inches; the soil varies from fresh lava to old well-disintegrated lava and alluvial valleys; the topography is rugged.

Practically all of the arable land of the lower elevations is cultivated.

Elimination of the undergrowth by man or grazing animals destroys the forest through exposing the trees and permitting the intrusion of Hilo grass.

The islands contain large numbers of endemic plants.

Only 6 strictly American genera occur in the Hawaiian Islands as compared with over 50 extra-American genera common to the islands and to regions of the Southern Pacific and Indo-Malaysia.

The large number of delicate forms whose seeds and spores could not survive transportation four or five thousand miles indicate a former land connection with the Southern Pacific islands. The ancient types forming the bulk of the vegetation have become more or less changed since the isolation of the Hawaiian Archipelago.